A meta-analysis of soil extracellular enzyme activities in response to global change

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ABSTRACT

The crucial biogeochemical processes such as carbon and nutrient cycling are increasingly altered at the ecosystem scale by global environmental changes. Although soil extracellular enzyme activities (EEAs) play a critical role in biogeochemical processes, the global patterns of soil EEAs in a changing world remain elusive. Here, we synthesized eight EEAs involved in carbon (C), nitrogen (N) and phosphorus (P) acquisition in response to seven global change factors based on 132 peer-reviewed papers. Our results showed that elevated CO_2 concentration had no significant effects on soil EEAs. Nitrogen addition stimulated C-acquisition (9.1%) and P-acquisition (9.9%) EEAs, but suppressed oxidase activity (-6.8%). Phosphorus addition decreased P-acquisition EEA (-19.8%), while combined N and P addition increased C-acquisition EEA (30.7%). Moreover, decrease in precipitation dramatically suppressed oxidase activity (-47.2%), increase in precipitation marginally stimulated N-acquisition EEA (16.7%), while warming significantly decreased oxidase activity (-10.9%) and had minor positive effect on hydrolytic enzymes. Overall, our results provide some evidence (with exceptions) for the resource allocation theory of microbial enzyme production, and indicate that EEAs are generally more sensitive to nutrient addition than to atmospheric and climate change. We have shown that global environmental changes can alter EEAs, which have implications for soil carbon storage, nutrient cycling, and plant productivity. Further research is needed to elucidate the underlying mechanisms driving the responses of EEAs to global change and to collect data from particularly non-forest ecosystems (e.g., wetland, tundra and desert) and global-change drivers (other than N addition) that lack of EEA data. Our synthesis of the responses of soil enzyme activities to global-change drivers can be used to develop better representations of microbial processes in ecosystem and earth system models.

1. Introduction

Human-induced global change including elevated CO_2 concentration, atmospheric nitrogen (N) and phosphorus (P) deposition, global warming, and altered precipitation has dramatically altered carbon (C) and nutrient cycling in terrestrial ecosystems. For instance, the annual N deposition is predicted to increase two or threefold in the future (Galloway et al., 2004) and this enhanced N availability can alter microbial community structure and activity, which has close connection with C and nutrient cycling (Janssens et al., 2010; Cusack et al., 2011; Leff et al., 2015). In the past decades, numerous field manipulation experiments have been well established worldwide to investigate the response of terrestrial ecosystems to global change. As a molecular protein that microbes produce to excavate nutrients for plant and their own growth, soil extracellular enzyme plays a critical role in biogeochemical processes as mediating the degradation, transformation and mineralization of soil organic matter (Sinsabaugh, 2010; Burns et al., 2013). In consequence, soil extracellular enzyme activities (EEAs) have gradually received attention and become an increasingly common tool for indicating microbial response to global change in field manipulation experiments (Weedon et al., 2011; Henry, 2012; Burns et al., 2013). These experiments were conducted in diverse ecosystems from arctic tundra to tropical forest, and various responses (positive, negative, neutral) of EEAs to nutrient or resource (C, N and P) addition and climate change (warming and altered precipitation) have been observed across different ecosystems globally (Henry et al., 2005; Allison and Treseder, 2008; Keeler et al., 2009; Turner and Wright, 2014; Meier et al., 2015).

The responses of soil EEAs to nutrient or resource manipulation are commonly explained by the "resource allocation theory" (Sinsaugh and Moorhead, 1994; Allison and Vitousek, 2005) which expresses that soil microbes regulate enzyme production based on the availability of resources. This microbial economic theory predicts that microbes would change their EEAs as a survival strategy – increasing EEAs in the presence of complex resource and decreasing EEAs when simple nutrient like inorganic nitrogen and assimilable carbon are available (Sinsaugh and Moorhead, 1994; Allison and Vitousek, 2005). This dynamic pattern has been demonstrated in incubation and greenhouse experiments (Allison and Vitousek, 2005; Stone et al., 2013) and also been observed in many field experiments. For instance, simple nutrients addition like inorganic N fertilizers are widely observed to stimulate phosphatase activity while inorganic P fertilizers consistently suppress it (Marklein and Houlton, 2012; Turner and Wright, 2014; Yokoyama et al., 2017). Moreover, elevated CO_2 could enhance belowground carbon input like dead roots and root exudates, which are considered as "complex nutrient" addition, and result in stimulation of C-acquisition EEA (Finzi et al., 2006; Meier et al., 2015). However, results inconsistent with this theory are also reported in previous studies (Saiya-Cork et al., 2002; Zeglin et al., 2007; Keeler et al., 2009; Dong et al., 2015; Jing et al., 2017).

The responses of soil EEAs to climate change (warming and altered precipitation) are dependent on the effects of climate change on soil properties, such as soil temperature and moisture, and availability of labile C, N and P resources (Henry, 2012). Soil warming can increase enzyme production if it enhances plant substrate input, but can also stimulate enzyme stabilization and turnover, and thus have an uncertain effect on the enzyme pool size which is the potential EEA measured under controlled conditions and common temperature in the lab (Henry, 2012; Burns et al., 2013). Additionally, soil moisture has been recognized as an important control of EEA at regional scale (Brockett et al., 2012). Increase in soil moisture should result in higher EEA, until the soil becomes anaerobic and substrate diffusion or oxygen content limits EEA (Henry, 2012). Therefore, water addition generally stimulated EEA, while rainfall exclusion or warming-induced drought often suppressed EEA (Allison et al., 2008; Kreyling et al., 2008; Sardans and Penuelas, 2010; Zhou et al., 2013). However, climate change also affects soil nutrient availability and other properties such as soil pH and microbial community, which may confound the direct effect of temperature and moisture on soil EEAs.

Given that soil EEAs were mediated by multiple factors (resource availability, environmental condition, and microbial community), the responses of EEAs to global change drivers remain poorly understood. In addition to numerous field experiments which measured soil EEAs in response to various global change drivers (Saiya-Cork et al., 2002; Henry et al., 2005; Finzi et al., 2006; McDaniel et al., 2013; Meier et al., 2015; Jing et al., 2017), a number of meta-analysis studies have synthesized the impact of global change on soil EEAs. For example, Kelley et al. (2011) showed that only chitinase activity consistently increased under elevated CO_2. Marklein and Houlton (2012) reported that phosphatase activity was enhanced by N addition, but suppressed by P addition. Jian et al. (2016) found that hydrolytic enzymes were enhanced, but oxidative enzymes were suppressed by N addition. Moreover, Henry (2012) and Ren et al. (2017) reviewed the responses of soil EEAs to climate change (warming and altered precipitation). These reviews and syntheses have greatly improved our understanding of soil EEAs to global change drivers. However, these studies used different criteria in their selection of data (field vs. lab and greenhouse manipulations, natural vs. agricultural ecosystems, C vs. N and P acquisition enzymes), and many field studies on soil EEAs in response to global change drivers have been published (including those published in Chinese literature) in the last 3–5 years.

Therefore, as a further development of these previous syntheses (Kelley et al., 2011; Henry, 2012; Marklein and Houlton, 2012; Jian et al., 2016; Ren et al., 2017), we performed a comprehensive updated global meta-analysis of the responses of soil EEAs to various global change drivers. We included six hydrolytic and two oxidative enzymes involved in C, N and P acquisition that are commonly measured, and seven global change drivers related to resource manipulation and climate change (elevated CO_2, N addition, P addition, combined N and P addition, decrease and increase in precipitation, and warming). Based on previous experimental and synthesis studies, we hypothesized that: (1) elevated CO_2 would stimulate EEAs because complex nutrients (plant-derived carbon substrates) were added, but N and P addition (simple inorganic nutrients) would suppress enzymes acquiring the added nutrients and enhance enzymes acquiring other nutrients; and (2) warming and increase in precipitation could increase EEAs, while decrease in precipitation could decrease EEAs.

2. Materials and methods

2.1. Data collection

Database in this meta-analysis was compiled by using Web of Science and CNKI (China National Knowledge Infrastructure) search engine (1900–2017). A total of seven experimental treatments were considered as global change factors related to nutrient addition and climate change. These treatments include CO_2 enrichment, nitrogen addition, phosphorus addition, combined nitrogen and phosphorus addition, precipitation decrease, precipitation increase and temperature increase. Additionally, data of eight soil enzymes and four soil properties were compiled from both control and treatment in these experiments. The eight enzymes include six hydrolytic enzymes, namely β-1,4-glucosidase (BG), β-D-cellobiohydrolase (CB), β-1,4-N-acetyl-glucosaminnidase (NAG), leucine amino peptidase (LAP), urease, and acid phosphatase (AP), and two oxidative enzymes, phenol oxidase (POX) and peroxidase (PER) (Table S1). The four soil properties, including pH, soil organic carbon (SOC), microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN), are only extracted from the papers containing EEAs and global-change treatments.

Proper papers were selected by meeting the following criteria: (1) only field experiments in natural terrestrial ecosystems were selected, while cropland, greenhouse and lab-incubation experiments were not included; (2) only corresponding nutrients (N and/or P) were added in the nutrient addition experiments (no other micronutrients were added); (3) the means, sample sizes, standard errors or standard deviations were reported; (4) if data from the same experiment were reported more than once at different time, only the latest data were selected; (5) data from only the surface soil layer were included; and (6) data were extracted either directly from tables and text, or indirectly by using software Engauge Digitizer from figures. In addition, experiment location, soil type, sampling depth and vegetation type were also extracted.

In total, 132 published papers (Appendix) meeting the criteria were selected for this study, including 1577 individual observations and 133 different sites mainly distributed over North America, Europe and East Asia (Fig. 1). Among the seven global change factors, N addition had the most data with 1056 individual observations from 70 different sites (Table 1, Fig. 1), while other global change factors were limited to < 200 observations from < 30 sites globally. As such, we further categorized data of N-addition experiments into four groups following similar work (Zhou et al., 2014; Jian et al., 2016): 1) ecosystem type (forest, grassland, tundra, wetland and desert); 2) fertilizer type (only NH_4^+, only NO_3^-, NH_4NO_3 and urea); 3) application rate (ranging from 5 to 600 kg N ha^{-1} yr^{-1}), which were divided into low (≤ 50 kg N ha^{-1} yr^{-1}), mid (> 50 and ≤ 100 kg N ha^{-1} yr^{-1}) and high (> 100 kg N ha^{-1} yr^{-1}) levels; and 4) treatment duration (ranging from < 1 to 19 years), which were divided into short (≤ 3 years), mid (> 3 and ≤ 10 years) and long (> 10 years) terms.